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A NEW DEVONIAN PELECYPOD FROM ALASKA AND ITS BEARING ON PTERIOID PHYLOGENY

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One of the most problematic aspects of a recent revision of some New York Upper Devonian pelecypods (McAlester, 1962a) was the generic status and phylogenetic position of the well-known Chemung stage pterioid species *Cornuellites* (formerly *Pterinea*) *chemungensis* (Conrad). This species is known only from the northern Appalachian region where it has long been considered to be an index fossil to the "type" Chemung (Chemung stage of Cooper, 1942; see also Williams, 1907, and Chadwick, 1935). Like most "index fossils," *C. chemungensis* first appears fully-developed in the stratigraphic record and then shows no evolutionary change before it disappears in late Chemung time. It is a common fossil at several localities which expose the middle Chemung stage horizons, but it is rare in the lowest and highest horizons of the stage. Most New York Upper Devonian clams have closely related species in the prolific earlier faunas of the New York Middle Devonian, but no probable ancestral or closely related species have been discovered for *C. chemungensis*. Furthermore, it is a morphologically distinctive species that can only with difficulty be forced into any of the standard genera of Devonian pterioids,

and for this reason it was very tentatively assigned to the Lower and Middle Devonian genus *Cornellites* in the revision of the Chemung faunas. This morphologic distinctiveness and apparent temporal and spatial isolation have combined to make the origins and relations of *C. chemungensis* most puzzling.

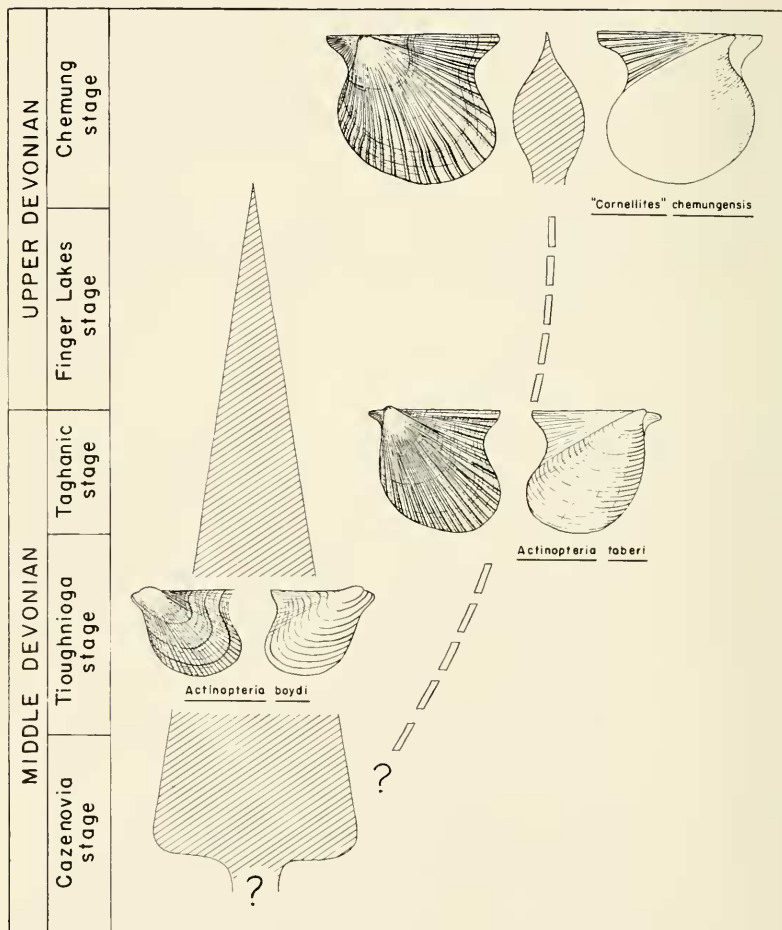


Figure 1. Suggested phylogenetic position of *Actinopteria taberi*. The shaded areas show known ranges and relative abundances of *Actinopteria boydi* and "*Cornellites*" *chemungensis*. The drawings of the species are schematic and are not intended to represent particular specimens.

Apr. 16, 1962 Devonian Pelecypod From Alaska

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Recently some unexpected new light has been thrown on this problem by several collections of poorly-preserved fossils found at Paleozoic outcrops which were exposed during highway construction operations near Livengood, Alaska. These specimens were collected by Bond Taber of the U. S. Geological Survey in the course of stratigraphic investigations in the Livengood region and were kindly sent to me for identification by R. B. Neuman and J. T. Dutro of the Geological Survey.

Pelecypods are the dominant element in the faunas from these outcrops, although some fragmentary gastropods, brachiopods, and crinoid columnals are also found. The pelecypods are of several types including schizodont, grammysoid, mytiloid, and other forms, but by far the most abundant and well-preserved element in these collections is a distinctive pteroid pelecypod which is described below as the new species *Actinopteria taberi*. This form is morphologically intermediate between the enigmatic *C. chemungensis* and the common Appalachian Middle Devonian species *Actinopteria boydi*. It therefore suggests that the Upper Devonian species "*Cornellites*" *chemungensis* may not be related to the Lower and Middle Devonian *Pterinea-Cornellites* stock as has long been assumed, but may instead have had an independent origin from an *Actinopteria* stock. The probable morphologic changes and time relations in this suggested phylogeny are shown schematically in fig. 1.

Mr. Taber anticipates further stratigraphic studies and fossil collecting in these rocks, and we hope that this work will provide additional specimens and data for a full description of the less common pelecypods of this significant fauna.

Actinopteria taberi, n. sp.

Figures 3-18

Description. Shell of medium size (median length of 14 measurable specimens 20 mm), inequivalve, left valve moderately convex, right valve slightly convex in umbonal region, becoming flattened towards margin. Shape variable, height ranging from 73 to 100 per cent of length (mean of 12 measurable specimens 80 per cent). Prominent anterior auricle and posterior wing on both right and left valves, relative length of both auricle and wing variable. Prominent radial surface sculpture on body of left

valve, becoming somewhat finer on posterior wing (figs. 3, 4). Well-preserved fragments of left valves show traces of very fine concentric sculpture (fig. 5). Surface sculpture of right valves consisting of strong radial ridges on posterior wing only, rest of valve showing faint radial and concentric sculpture making up fine reticulate network which is most prominent in umbonal region. Dentition and hinge features unknown. Ligament unknown. Musculature and interior features unknown. Shell material unknown.

Types. Holotype: U. S. National Museum No. 140873. Type locality: locality A (see below), near Livengood, Alaska. Stratigraphic position: probably near Middle-Upper Devonian boundary as defined in New York (see below). Additional specimens: U. S. National Museum Nos. 140874-140896 (No. 140897 questionably this species).

Material. The species is based on 18 relatively complete specimens (11 left and 7 right valves) and about 30 fragments. All of the specimens are preserved as predominantly external "composite molds" (see McAlester, 1962b). During diagenetic alteration the composite molds have become colored by a bright orange limonitic stain which clearly distinguishes the outlines of the former shell material against the much darker matrix. All of the specimens are permanently deposited in the U. S. National Museum, Washington, D. C.

Geographic occurrence. The species is known with certainty only from specimens found at the following two localities in the vicinity of Livengood, Alaska. Locality A (U. S. Geological Survey field locality number 60ATb85): medium bedded shale and siltstone from borrow pit on north side of Livengood-Eureka road approximately 7 miles southwest of Livengood, Alaska, Lat. $65^{\circ} 27'N$, Long. $148^{\circ} 43'W$, (N13.9 inches, E8.5 inches from SW corner measured parallel and perpendicular to west margin of Livengood B-4 quadrangle, Alaska, 1953 edition). Twelve relatively complete specimens and about 20 fragments were found at this locality. Locality B (U. S. Geological Survey field locality number 60ATb500): thin-bedded shales and siltstones with minor medium-bedded, medium to coarse-grained sandstone from borrow pit approximately 7.7 miles east of Livengood, Alaska, at approximately mile 61.4 on Elliott Highway (U.S. 97), Lat. $65^{\circ} 29.1'N$, Long. $148^{\circ} 21.7'W$, (N16.2 inches, E3.95 inches from SW corner measured parallel and perpendicular to west margin of Livengood B-3 quadrangle, Alaska, 1954 edition). Six relatively complete specimens and about 10 fragments were found at this locality.

Pteriod fragments also occur less commonly at several other borrow pits along the Livengood-Eureka road west of locality A. Unlike *A. taberi*, some of these specimens show right valves with strong, imbricate, concentric sculpture. Pending discovery of more material which would permit an analysis of variation in pteriods from these localities, only the specimens from localities A and B are included in *A. taberi*.

Stratigraphic occurrence. The following discussion of possible stratigraphic relations is based upon comments generously supplied by Mr. Taber who notes that there is considerable doubt about the age of the exposures from which the pelecypod faunas were collected. Mertie (1937) mapped the

outcrop areas of localities A and B as Devonian non-carbonate or intrusive rocks (Dnc, Dbi). The two nearest fossil localities mentioned by Mertie (p. 102 and 120) lie between localities A and B; Mertie's locality 16AMt64a was about 1½ miles southeast of Livengood, and his locality 21AMt128 was about 1½ miles south of Livengood. Both collections were made from limestone beds within essentially elastic sections that Mr. Taber feels are equivalent to each other and also approximately equivalent to the elastic sections in which the pelecypods were found. The fossils from Mertie's two localities (apparently mostly corals and brachiopods) were identified by Edwin Kirk, who regarded collection 16AMt64a to be Middle Devonian (Mertie, p. 103), while 21AMt128 was identified less definitely as "Devonian or Mississippian, more likely the former" (unpublished U. S. Geological Survey memorandum). Since Mertie's localities and the pelecypod bearing clastics may be equivalent, these identifications suggest a Middle Devonian or, perhaps, younger age for *A. taberi*.

The proposed phylogenetic position of *A. taberi* further strengthens this suggested age. The exact first appearance in the Appalachian Middle Devonian of *Actinopteria boydi*, the proposed ancestral form, has not yet been established, but it is extremely abundant in some lower Middle Devonian horizons, particularly the Delphi Station member of the Skaneateles formation (see Cooper, 1930, p. 219; also Cooper, 1942). It remains a locally common form throughout the New York Middle Devonian, but it becomes rare in the Upper Devonian where it is last known from only a few Chemung stage specimens. As mentioned earlier, the probable descendent species, "*Cornuellites*" *chemungensis*, is known only from the Upper Devonian Chemung stage of the New York region. These relations, which are summarized in fig. 1, are fully consistent with a late Middle or early Upper Devonian age for the Alaskan localities which contain the transitional *A. taberi*. It should be noted, however, that the Alaskan specimens could represent a later local survival of the transitional evolutionary stage and hence be contemporaneous with, or even younger than, the *C. chemungensis* bearing rocks of New York. On the other hand, a pre-Middle Devonian age would be most improbable for these localities if the proposed phylogeny is correct.

As noted below, slight morphologic differences in the specimens also vaguely suggest that locality A is the older of the two *A. taberi* occurrences.

Comparisons. *A. taberi* differs in the following ways from its nearest probable relatives:

Actinopteria boydi (Conrad): Left valves of *A. taberi* differ in showing coarser and more prominent radial sculpture and much finer concentric sculpture. Right valves of *A. taberi* show finer and more regular concentric sculpture, somewhat stronger radial sculpture on the posterior wing, and obscure traces of radial sculpture on the body. Both valves differ from *A. boydi* in having smaller but more sharply defined anterior auricles and a generally more upright shape.

"*Cornuellites*" *chemungensis* (Conrad): Left valves of *A. taberi* differ in having faint concentric sculpture and less widely spaced radial sculpture. Right valves of *A. taberi* have more prominent concentric sculpture and finer, less widely spaced radial sculpture on the posterior wing. Both valves have smaller anterior auricles and a less upright shape than *C. chemungensis*.

Discussion. "*Cornellites*" *chemungensis* and *Actinopteria boydi* are dissimilar enough so that the evolution of one from the other would not seem very likely were it not for the transitional Alaskan specimens. The evolution of *A. boydi* into *C. chemungensis* would primarily require an increase in size and erectness as well as a loss of concentric sculpture, a strengthening of radial sculpture, and a slight deepening of the "byssal notch" resulting in a more clearly-defined anterior auricle. An enlargement of the external ligament area and a strengthening of the dentition may have also been necessary, although too little is known of the hinge area in *A. boydi* to evaluate this possibility. As illustrated in fig. 2, the Alaskan

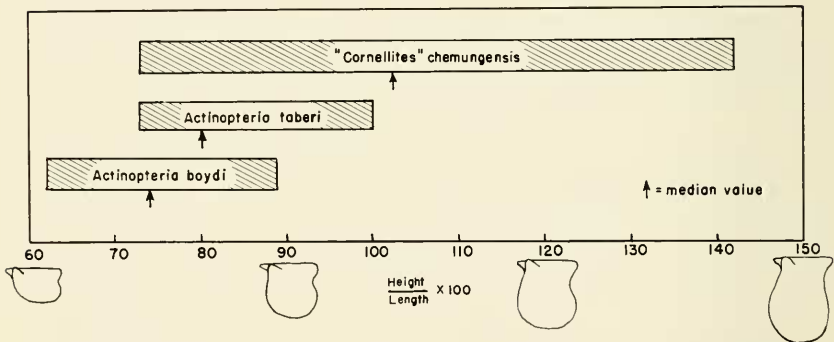


Figure 2. Range of shape variation in *Actinopteria taberi*, *Actinopteria boydi*, and "*Cornellites*" *chemungensis*. The data for *A. boydi* were based on 27 Yale Peabody Museum specimens from Pratts Falls, New York. The *C. chemungensis* measurements were taken from the 41 complete specimens described in McAlester, 1962a.

specimens are intermediate in erectness. They also show the expected strengthening of radial sculpture and weakening of concentric sculpture, as well as a more clearly-defined anterior auricle. *A. taberi* is not, however, completely ideal as a morphologic intermediate because several of the specimens show anterior auricles that are somewhat smaller than those of either *A. boydi* or *C. chemungensis*. This feature and other more minor differences caution that *A. taberi* may be somewhat removed from the direct evolutionary line between *A. boydi* and *C. chemungensis*.

There also appear to be morphologic differences in the material from each of the Alaskan localities, although too few good specimens are available to fully evaluate the consistency of this variation. Specimens from locality A (figs. 3-6, 8, 11-14, 16-18) are generally smaller, less erect, and show slightly finer sculpture than those from locality B (figs. 7, 9, 10, 15). The specimens from locality A are therefore most like the suggested stem form, *A. boydi*, whereas the locality B specimens are closer to *C. chemungensis*, the proposed descendent form. This tentatively suggests that locality A is the older of the two localities. More material might show these differences, if consistent, to be great enough for two specific names, but it now seems preferable to consider the specimens as one variable species. A single right valve found at locality B (fig. 19) is very erect and has a much larger anterior auricle than any of the other specimens from either locality. This specimen differs from the few known right valves of *C. chemungensis* only in having finer radial sculpture on the posterior wing with traces on the body of the valve. For this reason the specimen is doubtfully identified as *A. taberi* and was not included in the above species description. It may have come from a younger horizon than the other specimens found at locality B.

The dominance of *A. taberi* at these localities suggests similar associations dominated by "*Cornellites*" *chemungensis* in the New York Devonian which have been interpreted as "patch-reef" epifaunal assemblages adapted for life on hard shelly bottoms (McAlester, 1960). On the other hand, the fragmentary preservation of most of the Alaskan specimens also indicates probable strong current or wave action with transportation and perhaps mixing of the pelecypod faunas. Further ecologic interpretation may become possible with the discovery of new material and the description of the several less common pelecypods found at these localities.

No likely descendants of *C. chemungensis* are now known and therefore *A. taberi* and *C. chemungensis* may well form a compact and isolated evolutionary group. Normally it would be appropriate to propose a new generic name for these forms in view of their morphologic distinctiveness and probable evolutionary isolation. Because, however, of the current generic

chaos in the Paleozoic pteriod pelecypods, I prefer to avoid adding still another generic name without undertaking a more complete study of at least the Devonian pteriods. In any event, such nomenclatural matters are of minor importance in relation to the more significant evolutionary facts that they are intended to express. The transitional Alaskan specimens, which are clearly specifically distinctive, may of course with equal justification be assigned to the stem genus *Actinopteria* since they are morphological intermediates. This course is followed here pending more complete generic revision. It should be noted, however, that such revision will almost certainly result in a new generic name for "*Cornellites*" *chemungensis*.

Only one other New York Middle Devonian species is at all likely to have been ancestral to *C. chemungensis*. This is the common species *Cornellites* (formerly *Pterinea*) *flabella* (Conrad), which is undoubtedly closely related to the Rhenish Lower Devonian type species of the genus *Cornellites*. *C. flabella* shows some morphologic similarities with *C. chemungensis* (particularly the upright shape and the distribution of the sculpture on the right valve) but, in general, I regard the differences between these two forms to be even greater than those which separate *C. chemungensis* from *A. boydi*. Among the significant dissimilarities are the very strong reticulate sculpture, the proportionately larger and differently shaped auricles, and the strongly inflated left valve and strongly concave right valve. In particular the strong convex-concave shape appears to be an extreme specialization away from the more typical pteriod pattern of a slightly flattened right valve and a more gently convex left valve which is the pattern of both *A. boydi* and *C. chemungensis*. The evolution of *C. chemungensis* from *C. flabella* therefore now seems to me to be most improbable, based on our admittedly imperfect knowledge of New York Middle Devonian pelecypods.

The species is gratefully dedicated to Mr. Bond Taber of the U. S. Geological Survey to whom I am indebted not only for collecting the specimens, but also for valuable suggestions and enthusiastic cooperation. I also wish to express my appreciation to: R. B. Neuman and J. T. Dutro of the Geological Survey for first sending me the material; to my colleague K.

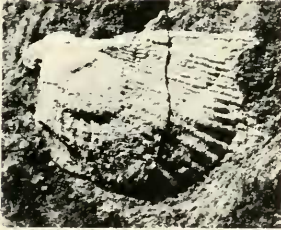
M. Waage for discussions and advice; and to John Howard and Bruce Umminger who carefully prepared the photographs and line drawings.

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Figures 3 - 11. *Actinopteria tuberi*, n. sp. All figures are left valves magnified x 1.5.

Figure 3. Holotype, USNM 140873, loc. A. Figure 4. USNM 140874, loc. A. Figure 5. Latex cast of USNM 140875, loc. A, a fragment of a left valve showing the concentric sculpture. Figure 6. USNM 140876, loc. A. Figure 7. USNM 140877, loc. B. Figure 8. USNM 140878, loc. A. Figure 9. USNM 140879, loc. B. Figure 10. USNM 140880, loc. B; the posterior and ventral regions are preserved only as a fragmentary negative composite mold and are therefore illustrated from a latex cast; the umbonal and anterior regions preserve the original positive composite mold. Figure 11. USNM 140881, loc. A.



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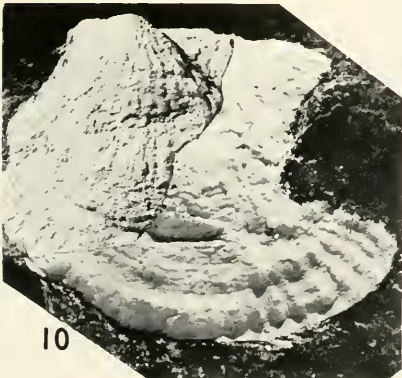
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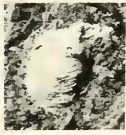
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Figures 12-18. *Actinopteria taberi*, n. sp. All figures are right valves magnified x 1.5.

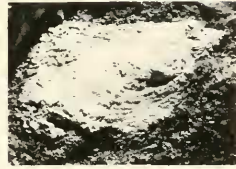
Figure 12. USNM 140882, loc. A. Figure 13. USNM 140883, loc. A.
Figure 14. USNM 140884, loc. A. Figure 15. Latex cast of USNM
140885, loc. B. Figure 16. Latex cast of USNM 140886, loc. A.
Figure 17. USNM 140887, loc. A. Figure 18. USNM 140888, loc. A.

Figure 19. ?*Actinopteria taberi*, n. sp. Right valve magnified x 1.5.

Figure 19. USNM 140897, loc. B, a doubtfully identified specimen
(see text).



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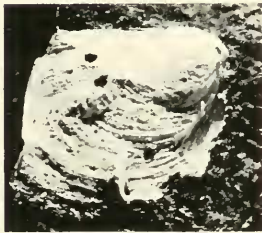
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